

Natural Dynamics of Population Structure and Habitat Use of the Lobster, *Homarus americanus*, in a Shallow Cove

ELISA B. KARNOFSKY, JELLE ATEMA, AND RANDALL H. ELGIN

*Boston University Marine Program, Marine Biological Laboratory,
Woods Hole, Massachusetts 02543*

Abstract. We report the results of a nonmanipulative field study of the lobster, *Homarus americanus*, using long-term behavioral observations of marked individuals. We observed a freely mobile population in an open shallow cove habitat (50 m × 150 m) in Buzzards Bay, Massachusetts. Lobsters larger than 50 mm carapace length (CL) living in or entering the study site were marked individually (334 during the 19-month study). Without further manipulation, the animals were observed as long as they remained in the study site. Of the marked animals, 48% were transient, *i.e.*, seen only once.

The population was made up largely of subadults with a sex ratio of M:F = 1.8. The summer and fall resident population consisted of about 30 animals. Maximum residency was over 13 months. Half of the resident population, mostly small animals (50–59 mm CL), apparently overwintered in the site. A distinct peak in molting occurred both years in the spring at a water temperature of about 15°C. Injured animals were seen frequently (26% of the population) including a high proportion of mature resident males missing claws. Most other injured animals were transient (60%). These results suggest that the shallow cove is used as a refuge for injured mature males.

Activity was strictly nocturnal with a peak 1–3 h after sunset and declining through the night. Activity levels were equal for both sexes. Overall activity was correlated with seasonal variations in water temperature (0–24°C). At times, activity was correlated more with molting (pre-molt activity peak) than with temperature. Behavioral interactions in this population are described in a companion paper (Karnofsky *et al.*, 1989).

Introduction

The lobster, *Homarus americanus* (Milne-Edwards), is a slowly maturing, exceptionally long-lived, marine invertebrate inhabiting a large and varied geographic range from Newfoundland to Cape Hatteras, and from the low tide mark to the submarine canyons off the Continental Shelf at 400–600 m (Phillips *et al.*, 1980; Cooper and Uzmann 1980). This species is important both for scientific and commercial reasons. It supports a major fisheries in Canada and the United States and considerable effort has gone into its culture. Scientific investigations using lobster models range from studies on neurotransmitters, developmental neurobiology, and chemoreception to ecological models. Yet detailed knowledge of the natural behavior of *Homarus americanus* is sparse (reviewed by Atema and Cobb, 1980, Atema, 1986). Tag-recapture studies and submersible and SCUBA diver surveys provide some information about natural history, geographic range, and sex and age distribution in lobster populations (reviewed by Cooper and Uzmann, 1980; Campbell, 1986; Campbell and Stasko, 1986; Munro and Therriault, 1983; Pezzack and Duggan, 1986). Habitat may influence various aspects of behavior, population structure, and perhaps even social organization. Most field studies to date have relied on manipulations of either the population (Stewart, 1972; Hudon, 1987) or the habitat (with respect to artificial shelters, Scarratt, 1968; Sheehy, 1976) or both (O'Neill and Cobb, 1979). Such manipulations could affect the behavior of the population. Two previous studies in the field looked at long-term shelter occupancy: Stewart (1972) recognized residents, animals seen several times in a small area; Ennis (1984) found similar patterns and used the term territoriality to describe these types of habitat use. However, we

prefer to use the commonly accepted definition of territoriality as defense of an area.

In 1978 we began a long-term field study in an area suitable for continuous, detailed observation throughout the seasons, restricting manipulation to marking individuals. There was no interference with the structure of the landscape. Since year-round observations of nocturnal marine animals are difficult, we chose a remote shallow cove where we could use snorkle rather than SCUBA to maximize data collection and to minimize disturbance by divers. In addition, the remoteness and shallowness of the site minimized interference from lobster fishing.

The aim of this study was to gain insight into the factors determining population structure and behavior in a society of unmanipulated, freely interacting lobsters. These field studies were complemented by laboratory studies in large naturalistic aquaria (Atema *et al.*, 1979; Atema, 1986). This paper describes the habitat, the structure of the lobster population, and the way it uses the shallow cove habitat; a companion paper describes the behavior of the lobsters in this population (Karnofsky *et al.*, 1989). Preliminary results of this study were reported in Karnofsky and Atema (1979).

Materials and Methods

The habitat

The field site was a shallow cove of about 50 m \times 150 m along a tidal channel in Buzzards Bay near Woods Hole, Massachusetts (Fig. 1). Lobster shelters were found in water depths ranging from 0.3 to 1.5 m at mean low tide. The site experiences about 1 m of tidal fluctuation and a mean tidal current of about 1 km/h. The substrate consisted of mud and sand with eelgrass, bare sand, and rocks covered with macroalgae ("rock garden" Fig. 1). It sloped gently to a greater depth toward the channel. In winter and early spring the eelgrass was only about 10 cm long and sparse. Craters of 10 cm depth marked the location of collapsed eelgrass shelters from previous years. In various places in the eelgrass, furrows were gouged by ice flows. In the rock garden, sand was carried into shelter openings by winter storms. As summer progressed, the eelgrass grew to a length of 1–1.5 m. Their blades became a flat, impenetrable mat in the tidal currents, particularly at low tide. The channel connects two water basins, Buzzards Bay and Vineyard Sound, with different tidal cycles resulting in strong currents (up to 6 km/h) during times of high and low water. Along the channel the cove was delineated by an abrupt drop-off providing a bank, which was inhabited by larger lobsters. This area was not included in observations. Seasonal water temperature ranged from 0° to 24°C (Fig. 2A).

Data collection

Extensive preliminary studies were made in 1978 and 1979 to determine feasibility and to develop non-invasive methods. Observations with standardized procedures were made over 19 months, from 1 January 1980 to 31 July 1981, 1–6 times per week, depending on weather, and 1–4 h per night depending on water temperature and available observers, making up 333 hours of observation (Fig. 2B). For each observation period, tidal height, water temperature, underwater visibility, wind and wave action, and changes in flora and fauna were recorded. Observations were made almost exclusively by surface snorkling. Nearly all lobster activity was observed at night using hand-held, dim-white flashlights with narrow beams. Underwater notes were written with pencil on sanded pieces of plexiglass. Almost all observations were made between one hour after sunset and one hour before sunrise, with emphasis on the period of highest activity (1–3 hours after sunset; Karnofsky *et al.*, 1989). Observations were biased towards areas of higher lobster density and activity, but the entire area was searched at regular weekly intervals. High tide observations were difficult, especially on nights with poor visibility caused by storms and plankton blooms, and were therefore less frequent than low tide observations. Winter observations from January to March 1981 were nearly absent due to storms and ice.

All lobsters > 50 mm carapace length (CL) were caught once by hand or net, marked and described individually, and released at the exact site of capture a few minutes later. They were recaptured and rebanded after molting. During the 19 months of standardized observation, 334 lobsters were marked on the night of their first sighting. Marking consisted of placing one red and one white rubber band behind the dactyl on each claw where they do not interfere with claw use. Each band was printed with the lobster's identification number. A white band on the left claw marked females, on the right, males. Preliminary observations had shown that this method of numbered, color-coded claw band marking was effective for quick identification of individuals, especially during nighttime observations, both inside and outside the shelters. Lobsters in shelters often had their claws showing at the entrance. In addition, the heavily calcified claws of a molt shell remained intact for several days (longer than other shell parts) and helped to determine an individual's time and place of molt. To estimate the date of a molt, information was combined about when, where, and in what condition the molt shell was found, the last day the animal was seen, and its carapace hardness when it was recaptured. Growth was determined by comparing the length of the carapace before and after molt.

To further mark each individual, we also clipped some

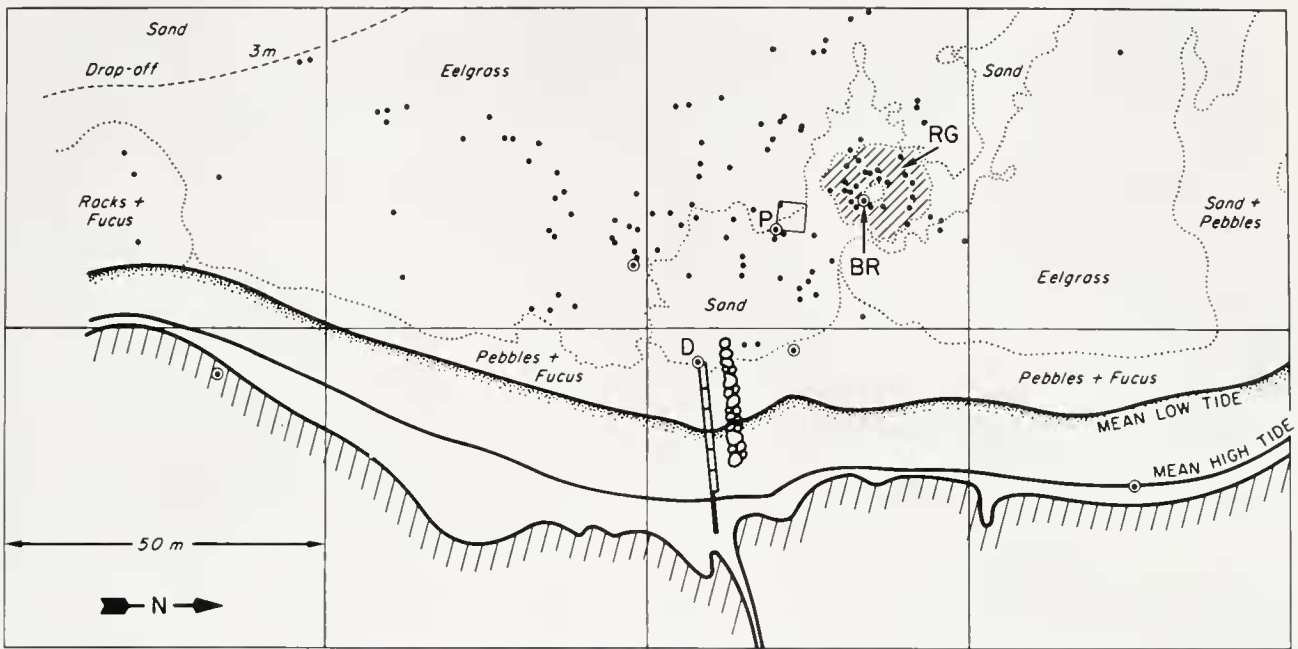


Figure 1. Map of field site showing substrate features and location of lobster shelters. Locations of prominent shelters and frequently used shelters are indicated with a dot. These shelters were individually labeled. D, dock; P, 4 × 4 m marked plot; BR, big rock; RG, rock garden (cross hatched). Grid 50 m. This map of shelter locations was drawn in 1979 using triangulation from fixed points on the shore and in the site (circled dots).

of the ten pleural points along the ventral abdomen in specific combinations. These clip marks remained visible for one or two molts. After 1–2 weeks of shell hardening, molted lobsters were re-marked with the same pleural clip code and a new band number. The description of marked lobsters included sex, size (CL in mm), left or right handed position of the crusher claw, exact time and location of capture, hardness of carapace, and other distinguishing characteristics such as missing appendages, scars, or growth of barnacles. Lobsters < 50 mm CL were marked periodically with a telson clip without regard to individual, sex, or size. Other interference with the lobster's behavior was avoided. During observations the location and activity of all marked lobsters were recorded. Unless otherwise stated, the group of individually marked lobsters larger than 50 mm CL is referred to as the "population."

The most frequently used home shelters were labeled by placing rocks with numbers painted on them next to the shelter opening, and the condition of these shelters was recorded regularly. New shelters were numbered as they appeared.

Results

Shelter

Approximately 130 shelters were marked during the study. Shelters were found either among small boulders

(0.1–2.5 m diameter) where lobsters occupied crevices and holes repeatedly, or in the eelgrass burrowed under the roots. The presence of lobster shelters was usually revealed by a characteristic pile of freshly moved sand. Shelters often had two openings: one major entrance and a smaller "escape" door. Shelter openings were not oriented in any specific direction; for instance, they were not aligned with the tidal currents.

Residency

The individual lobsters making up the population of the cove were continually changing. Some lobsters were seen only once and considered "transient," whereas any lobster seen more than once was called "resident." Of the 334 marked lobsters, 174 were residents (52%) and 160 were transients (48%). The maximum residency period was greater than 13 months.

Not every resident was observed during each observation period; some were not seen for days or weeks. They may have escaped observation or left the area temporarily. To estimate the resident population, we adopted the following criterion for presence in the area. The mean and standard deviation of the longest gaps between sightings of each resident was 32 ± 9 days. Using this mean, plus one standard deviation, we considered a lobster to be present in the area if the sightings were not more than

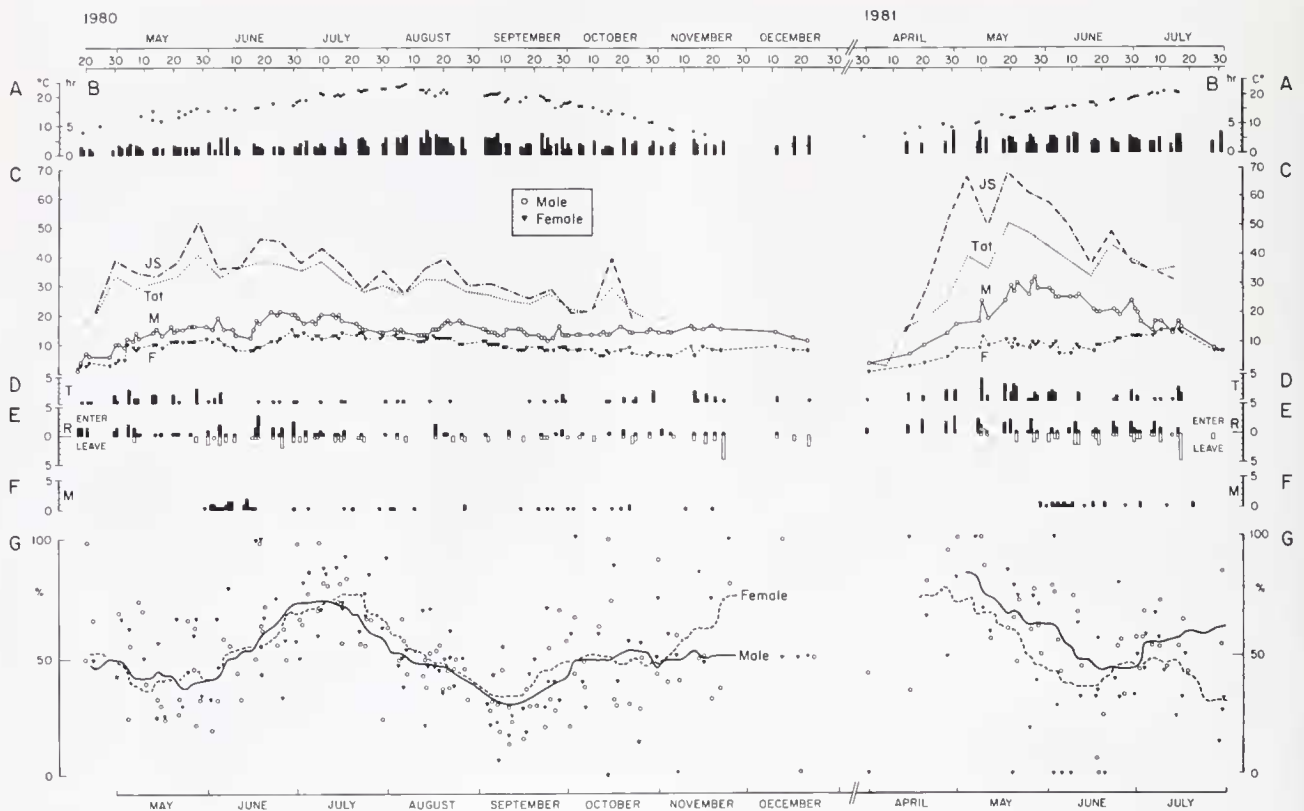


Figure 2. Seasonal description of daily lobster population. Due to weather, winter observations were sporadic and are not included in the figure. A. Water temperature (dots); left side of vertical scale indicates °C. B. Daily observation hours (bars); right side of vertical scale indicates daily number of observation hours. C. Population size: Calculations of daily number of males (M) and females (F) in the site (if an animal was seen within 41 days of its last sighting it was assumed to be a resident of the site, see text); calculation of weekly total number of all animals (Tot)—for this, each animal was counted only once per week; and Jolly-Seber estimate (JS) of weekly population size. *Note:* data after 20 June 1981 (*i.e.*, 41 days prior to the end of the study) are necessarily incomplete with regard to residency; thus population estimates are probably considerably below the actual number of animals present: some animals that were scored as “transients” (D) or “residents leaving” (E) would have been scored as residents if they had been observed again within a 41-day period after the end of the study on 31 July 1981. D. Daily number of transient lobsters (T). Transients were lobsters seen only the night of their initial marking. (See Note in C.) E. Daily number of resident lobsters (R) entering and leaving. Black bars upward: number of residents entering (the night of their initial marking); white bars downward: number of residents leaving (the night of their last sighting). Residents were lobsters seen during more than one night. (See Note in C.) F. Daily number of molting animals (M). Dates could be estimated, often precisely, from last sightings, post-molt recaptures and molt remains. G. Daily mean activity of males and females plus 28-day moving averages. Activity was calculated as the fraction of lobsters observed outside of shelter over the total number observed that day, based on daily first sightings of individuals only. ○ = Male, ▼ = Female.

41 days apart. Only 4 lobsters seen more than once had gaps between sightings longer than 41 days.

Based on these criteria for residency, the daily resident population size was determined separately for males and females (Fig. 2C; M, F). In addition, the total population per week was estimated (Fig. 2C; Tot). Weekly estimates were based on the total number of different individuals observed in the cove during one week regardless how many times an individual was sighted. This number cannot be derived from the addition of daily male and fe-

male totals, due to varying numbers of transients (Fig. 2D) and to residents entering and leaving (Fig. 2E). The resulting seasonal population curve of weekly estimates was closely approximated by weekly estimates calculated from the Jolly-Seber recapture model (Jolly 1965; Begon 1979) (Fig. 2C; JS). The Jolly-Seber model determines population size while taking into account transient animals. The population reached a peak of about 40 in June, of which about 30 were residents. The population then decreased gradually

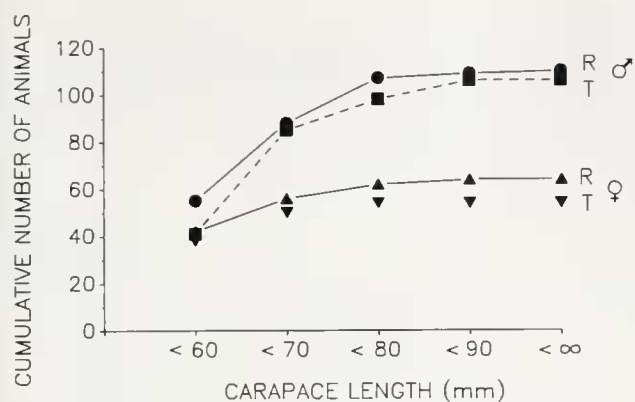


Figure 3. Cumulative size-frequency distributions for sex/residency groups based on size at which animals first entered the marked population (*i.e.*, not using their post-molt size). Smallest size class (<60) comprises animals 50–59 CL; next size class (<70) animals 50–69 mm CL, etc. Animals > 70 mm CL are considered mature. R = resident; T = transient.

through the summer and fall to about 15 residents in winter (see “overwintering” below).

Sex ratio, size distribution, molting, and growth

Throughout the year there were always more males than females (overall sex ratio M:F = 1.8). The sex ratios in the resident and transient group were similar (1.7 and 2, respectively) and did not change with seasons.

Size-frequency distributions were determined in 10 mm CL size classes for male and female residents and transients (Fig. 3); for lobsters of this size, 10 mm CL represents roughly one molt increment (see below). More than half of all marked lobsters were in the 50-mm CL size class (*i.e.*, 50–59 mm CL). Considering the overall sex ratio, females were over-represented in the 50 mm CL size class: this class contained 67% of all observed females but only 42% of all males (*t*-test, $P < 0.05$). Estimating that in the study area maturity both for males and females is reached between 70–80 mm CL (Estrella and McKiernan, 1986), 20% of the marked male population and only 10% of the female population was considered to be mature. The largest lobster was a 92-mm CL male. Thus, all calculations show that in this population the males were not only twice as common, but also relatively larger.

Sixty-six lobsters molted during the study period, 42 of them in a two-week period in spring of both years (Fig. 2F). We observed a peak of 23 molts between 31 May and 11 June 1980 and another peak of 19 molts between 29 May and 16 June 1981. In both years, in the month before the spring molt peak there was an influx of transients (Fig. 2D) and residents (Fig. 2E). Many residents left the area during and following the molt peak. There

was no evidence of these animals molting a second time in the cove. Both the sex ratio and the size distribution of molting lobsters were similar to those of the total population.

Not all lobsters were recaptured after their molt. The mean premolt size of lobsters that remained in the site and were recaptured after molting was significantly smaller (57.4 mm CL for males; 58.2 mm for females) than the mean size of those that were not recaptured (64.5 mm for males; 63.3 mm for females) (*t*-test; $P < 0.05$). Only 3 of 28 animals in the smallest size class were not recaptured after molting, compared to 9 of 19 animals of 60 mm CL and larger. Twelve of 28 small animals and only 1 of 19 larger animals remained in the site for more than 25 days after molting; the difference is significant (G-test, $P < 0.01$). This indicates that after molting, larger animals leave the area sooner (or, less likely, that they become more elusive).

The average growth per molt was 9.6 mm CL (17% increase). There was no difference between males and females: growth per molt averaged 9.8 mm (17%) for males, and 9.3 mm (16%) for females. There was a significant seasonal difference in growth per molt (*t*-test; $P < 0.05$), with the largest increase observed in spring 1981 (11.7 mm; 19%). The smallest increment observed was 8% in a female of 51 mm CL (fall 1980), possibly caused by regeneration of a seizer claw.

Injury

Various minor injuries were seen: *i.e.*, puncture wounds, clipped or missing antennules and antennae, and missing walking legs. Ninety lobsters (27% of the marked population; Table IA) were missing one or both claws when first sighted, or, in seven cases, following their molt. Crusher claws were missing in 48 animals, seizer claws in 37, and 5 animals were missing both. The incidence of claw loss (Table IB) was greatest among large resident males (41%), followed by small transient females and males (38 and 35%, respectively). Claw loss was least frequent among large resident females (13%), followed by small resident males and females (17 and 18%, respectively). The difference in claw loss frequency between small (immature) transients and small (immature) residents is significant (G-test, $P < 0.001$), but the difference between large (mature) resident males and females is not significant (G-test, with Yates correction for small samples; $0.1 > P > 0.05$) (Table IA) probably due to the small sample size.

Activity

We determined lobster activity levels during the nighttime observations as did Ennis (1984), by dividing the number of times each individual lobster was seen outside

Table I

A. Incidence of claw loss: distribution of animals missing crusher claw (C) or seizer claw (S) or both claws (C + S), among resident (R), transient (T), male (M) and female (F) lobsters

	C	S	C + S	Totals	
R M	11	12	1	24	
R F	7	3	1		11
					35R
T M	19	14	2	35	
T F	11	8	1		20
					55T
Totals	48	37	5	59 M	31 F = 90

B. Incidence of claw loss: distribution of claw loss (C, S, C + S) among small (immature) and large (mature), resident (R) and transient (T), male (M) and female (F) lobsters

		n/N	(%)	Total	(%)
Small (<70 mm CL)	R M	15/88	(17)	25/144	(17)
	R F	10/56	(18)		
	T M	29/82	(35)	48/132	(36)
	T F	19/50	(38)		
Large (>70 mm CL)	R M	9/22	(41) *	10/29	(34)
	R F	1/7	(13)		
	T M	6/24	(25)	7/28	(25)
	T F	1/4	(25)		

n/N = Number of animals with one or two missing claws as a fraction of the total for the group.

** = Significant difference (G-test, $P < 0.001$).

* = Not significant (G-test with Yates correction for small samples; $0.1 > P > 0.05$).

a burrow by the number of times it was seen anywhere. The results were similar whether we used first nightly sightings of individuals or all nightly sightings. A 28-day moving average drawn through the points (Fig. 2G) showed no difference between the activity of females and males. Activity did not follow water temperature: decreasing activity in May and late July and August coincided with rising temperature, and increasing activity in October and November coincided with decreasing temperature. In 1980 the periods of low activity fell just before the spring and fall molt peaks; this was not the case in 1981. Although water temperature patterns in 1980 and 1981 were very similar, there were differences in activity patterns (Fig. 2G), indicating that temperature above 10°C did not predict activity as closely as found by Ennis (1984).

There was a pronounced circadian activity pattern. Lobsters were rarely seen during the day; they remained deep in their shelters. At sunset some began to appear at shelter opening, claws out. Most would not actually leave until about one hour later. The moving averages were used to determine whether nightly activity was related to time of night, and/or tide height or direction. Points falling above or below the moving average of Fig-

ure 2G indicate more or less than average activity. Above-average activity was more common during sunset observations (*i.e.*, 1–3 h after sunset) while below-average activity was more common during the less frequent sunrise observations (*i.e.*, 1–3 h before sunrise) (Table II). The correlation with time of night was significant: lobsters were most active between one and three hours after sunset. Generally they walked around slowly, checking shelters, interacting, and feeding. Activity decreased during the night with the lowest point being one to three hours before sunrise. Males and females, analyzed separately, behaved similarly. Although not statistically significant, a trend toward greater activity occurred during the less frequent high tide observations and a trend toward lower activity during low tide observations. The direction of the tide, *i.e.*, rising or falling, showed no effect on activity.

Overwintering

During the few winter observations it appeared that lobsters hardly moved at water temperature below 5°C. One stiff-legged, barely walking animal was observed out of shelter in January 1980 at 5°C. About one half of the

Table II

Lobster activity: nightly and tidal changes

	Time of night			Tide			
	Sunset	Midnight	Sunrise	High	Low	Rising	Falling
Above avg.	43*	5	1*	15	35	32	23
Below avg.	25*	10	10*	7	42	20	28

* = Significant difference (χ^2 , $P < 0.05$).

The number of points above and below the moving average of Fig. 2G are listed; each point represents the relative activity (%) of the population for that observation day, based on first sightings of individuals only (see text).

resident population (10 males, 5 females) were seen in late fall 1980 and again in 1981. In spring, 12 of these were in the same area (about 10×10 m) where they were last seen in late fall; 4 of these animals occupied the same 4 shelters before and after the winter. Two were males larger than 70 mm CL, and the remaining 13 animals were in the 50-mm CL size class. Nine of the 15 lobsters were observed well before the water temperature reached 10°C in April. The 15 lobsters probably overwintered in the cove. Later, 12 of them molted in the observation area. Five of these 12 had molted there in the previous fall.

Discussion

The data collected in this long-term study on a population of individually marked animals revealed several new and important aspects of the habitat use and population dynamics of *Homarus americanus*. These include long term residency, overwintering in shallow water, possible reasons for observed sex ratios, and a "refuge" function of the shallow habitat. It would be premature to generalize results which are determined at least in part by the habitat. Comparison with other habitats will be needed.

Although there was a steady stream of transient lobsters (as described by Stewart, 1972; Ennis, 1984), many lobsters were residents for considerable periods of time (months) in this shallow habitat. We had not suspected previously that so many animals lived in such shallow water (less than 1.5 m), let alone that they might overwinter there. It appears that at any one time in summer, at least 30 animals resided in the cove, concentrated in the rock garden and a few small peripheral areas of eelgrass. The weekly estimates were higher because they included individuals passing through the cove during the week. Although large lobsters were described in extremely shallow water during the 17th century (see Wood, 1967), lobsters, particularly large ones, are now rarely seen there. This may be due to fishing and/or increased human use of the shore line. The isolation of our shallow site may have contributed to its population den-

sity. However, perhaps the lack of daytime activity of lobsters in such shallow water has made them difficult to spot.

In winter, the number of residents appeared to decline to about 15. In keeping with the objectives of our study (*i.e.*, no disturbance except banding), we did not dig out overwintering lobsters to prove their presence. However, we consider the indirect evidence sufficiently strong to indicate shallow water overwintering by mostly small lobsters. Rock shelters are relatively safe from ice damage; overwintering in rock shelters may be an alternative preferable to the dangers of migration, such as exposure to predation and competition for shelters both elsewhere and upon return. Such dangers may apply particularly to smaller lobsters, which may not migrate as efficiently, and would suffer most from both predation *en route*, and shelter competition on arrival. Thomas (1968) described lobsters overwintering in 1.3–4 m of water in the mouth of the Bideford River, Prince Edward Island, Canada. Overwintering was common in Ennis' (1984) study, but the depth of winter shelters was not recorded and could have been down to 25 m.

A stable feature of the population was the male-biased sex ratio of about 2 (Fig. 3). The same ratio applied to various subpopulations, *i.e.*, resident, transient, molting, overwintering, and injured animals. Predominantly male populations were observed using trap statistics in shallow waters (4–10 m; Briggs and Mushacke, 1979) and in shallow artificial reefs (3–6 m; Zawacki, 1971; Briggs and Zawacki, 1974). In contrast, studies in deeper water (up to 24 m) have shown a 1:1 sex ratio (Krouse, 1973; Stewart, 1972; Cooper *et al.*, 1975) or even a predominance of females (Briggs and Mushacke, 1979; Estrella, 1983; Cooper *et al.*, 1975). The overall sex ratio of commercial catches is 1:1 (Cooper and Uzmann, 1980). The causes of the male-biased sex ratio in shallow water are not clear. We believe it could result from both behavioral-genetic and man-made factors. Natural lobster behavior could force mature males that lost competition for mating shelters (Atema *et al.*, 1979; Atema, 1986;

Karnofsky and Price, 1989) to move into more shallow areas; this fits with our observation of disproportionate claw loss of resident mature males in the shallow site and a limited number of mating shelters (Karnofsky *et al.*, 1989). For the same reason, maturing females may prefer to leave the area and move to deeper water because of the greater number of dominant males and mating shelters available for mating cohabitation. Mature females are protected by males during a cohabitation period surrounding their molt (Atema *et al.*, 1979; Atema, 1986). Deeper water might also protect female lobsters with externally carried eggs from storm-generated changes in salinity, turbidity, and temperature. In a Xanthid crab, Hazlett *et al.* (1977) found egg-bearing females in deeper water than females without eggs. In addition, since shallow waters are not fished, the relatively larger number of females in deeper water may be due to greater fishing pressure on males; deeper water is heavily fished, but egg-bearing females are protected from fisheries.

We noted that lobsters of all size classes moved into and out of the site. Our study only documented those larger than 50 mm CL. These animals could be recruited either from a resident population of smaller animals molting into the observed group, or from transient animals moving in from other locations. Both types of recruitment appear to occur. Some of the <50 mm CL lobsters that we telson-clipped without regard to sex or size subsequently molted into the observed population.

After the spring molt peak, all molted lobsters gradually left the study site. None of these animals molted a second time in the cove. Given the higher postmolt recapture rate for immature (<70 mm CL) lobsters, mature lobsters (>70 mm CL) may have left sooner after molting than the smaller ones. The general pattern of behaviors associated with the fall molt peak were similar to the spring molt peak except that not all lobsters left the cove following their molt. Of these, many were seen the following spring and some molted again in the cove during the spring molt peak before leaving.

A dramatic feature of the population was the large number of injured animals: 26% of the animals marked during the study were missing one or both claws. This was far more than the 15% claw loss determined in nearly simultaneous trap surveys of lobsters in Buzzard Bay (Estrella, 1983). Even in a Canadian habitat where algal harvesting caused general damage to lobsters, claw loss was only 14%, and this was double that of the normal incidence reported for that area (Scarratt, 1973). The great incidence of claw loss in our study suggests that this shallow site could serve as a refuge area for damaged animals perhaps escaping intraspecific competition.

Most animals with missing claws were small transients; however, among residents mature males missing claws were disproportionately represented (Table 1B).

Similarly, Moriyasu (1984) reported that the percentage of lobsters missing claws increased over the summer in the Bidford River estuary reaching 30–40%, and that most of the large lobsters missing claws were males. Fishermen in that area suggest that lobsters missing claws move into the estuary (“hospital area”) to regenerate. Since mature males compete for shelters that allow them to attract females (Atema, 1986; Karnofsky and Price, 1989) the losers of intrasexual competition may retreat to shallow water where competition for proper shelter is reduced. Lobsters missing one or two claws show increased tendency to flee when challenged (O’Neill and Cobb, 1979), but small animals rarely challenge large ones. Thus, because few large animals live there, the shallow habitat may serve as a refuge area for larger male lobsters missing claws. The smaller injured animals at our site were mostly transients. Since half the resident population in the cove was in this size class, this may reflect stronger competition between animals close in size as seen in staged laboratory fights (Scrivener, 1971). Similarly, brachyuran crabs of similar size show increased aggression (Sinclair, 1977) and when of markedly different size ignore each other (Vannini, 1980). However, social interactions are not the only causes for claw loss. Lobsters too small for commercial use can be damaged in traps before, during, and after they are released. Lobsters are also vulnerable following their molt, as illustrated by the seven lobsters newly missing claws after molting. Missing appendages may also be due to fish predation (A. Richards, pers. comm.).

Many lobsters molted during the first two weeks of June (Fig. 2F). This spring molt peak is probably the result of endocrine synchronization caused by the rise in water temperature to 10°C (Fig. 2A), coupled with increased photoperiod (Aiken, 1980). In both years, the number of transient lobsters increased during the month before the spring molt peak (Fig. 2D). These may have been lobsters looking for shelter in which to molt, but who were unable to establish residency due to intraspecific competition; both the overall population size had increased (Fig. 2C) and premolt residents may be more active and aggressive, as shown in laboratory studies (Tamm and Cobb, 1978).

In our marked, mostly immature population all lobsters had an equal probability of molting, and males and females grew equal amounts in a single molt. Our growth data were obtained from single molts per individual, unlike previous tag recapture studies which always lack direct information on the number of molts for a given individual. While we found no significant difference between male and female growth, most of these other studies indicated greater male growth (Ennis, 1972; Cooper and Uzmann, 1971; Squires, 1970; Wilder, 1953, 1963; Campbell, 1983); only Cooper (1970) found no difference in

growth increments between sexes. The difference may be explained by sexual dimorphism in growth beginning to manifest itself at maturity (Templeman, 1935). Reduced growth in mature females may be caused by egg production (Squires, 1970). We would not see these effects in our study because most lobsters, particularly females, were immature, although female courtship behavior (Atema *et al.*, 1979) and ovarian development (review in Aiken and Waddy, 1980) may already begin in the 60-mm CL size class. In the population of our shallow site, males and females were almost equally represented among the 50–60-mm CL sized animals; however, females became increasingly less represented in the larger size classes (Fig. 3).

The shallow cove study site is only one of many different lobster habitats. Because of the shallow water depth, the elements (wind, sun, and ice) greatly affect the environment. In early spring lobsters could easily maneuver through the short eelgrass. Furrows carved out by winter ice provided starting places for burrowing under the eel grass roots. The rock garden was less affected by ice, but storm-induced sand-shifts often obstructed or uncovered the shelter openings. In summer the eelgrass grew into a dense mat, particularly impenetrable during the high currents at low tide. Many eelgrass shelters were abandoned and eels were often seen in the shelters unoccupied by lobsters. Such interspecific shelter competition may have contributed to the overall decrease of the lobster population over the summer (Fig. 2C).

In this shallow site lobsters were very rarely active during the day; they stayed deep in their shelters. In deeper water where the light level is lower, lobsters have been seen out of shelter during the day (Dr. Richard Cooper, pers. comm.). In our study, lobsters were most likely to be away from their shelters between 1 and 3 hours after sunset. Activity decreased during the night with a low point 1–3 hours before sunrise. This differs from a laboratory report of both post-sunset and pre-sunrise activity peaks (Cobb, 1969). Ennis (1984) found circadian activity peaking 2–3 hours after darkness, gradually dropping to very low before dawn and absent during the day. Similar results were reported by Cooper and Uzmann (1980). Our data also showed a tendency toward greater activity at high tide: in our site, the strong currents at low tide may hamper lobster movements and increase their vulnerability to predators.

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Literature Cited

- Aiken, D. E. 1980. Molting and growth. Pp. 91–163. in *The Biology and Management of Lobsters*, Vol. 1., J. S. Cobb and B. Phillips, eds. Academic Press, New York.
- Aiken, D. E., and S. L. Waddy. 1980. Reproductive biology. Pp. 215–276 in *The Biology and Management of Lobsters*, Vol. 1., J. S. Cobb and B. F. Phillips, eds. Academic Press, New York.
- Atema, J. 1986. Review of sexual selection and chemical communication in the lobster, *Homarus americanus*. *Can. J. Fish. Aquat. Sci.* **43**: 2283–2290.
- Atema, J., and J. S. Cobb. 1980. Social behavior. Pp. 409–450 in *The Biology and Management of Lobsters*, Vol. 1., J. S. Cobb and B. F. Phillips, eds. Academic Press, New York.
- Atema, J., S. Jacobson, E. Karnofsky, S. Oleszko-Szuts, and L. Stein. 1979. Pair formation in the lobster, *Homarus americanus*: behavioral development, pheromones and mating. *Mar. Behav. Physiol.* **6**: 277–296.
- Begon, M. 1979. *Investigating Animal Abundance: Capture-recapture for Biologists*. University Park Press, Baltimore. 97 pp.
- Briggs, P. T., and F. M. Mushacke. 1979. The American lobster in western Long Island Sound. *N. Y. Fish Game J.* **26**: 59–86.
- Briggs, P. T., and C. S. Zawacki. 1974. American lobsters at artificial reefs in New York. *N. Y. Fish Game J.* **21**: 73–77.
- Campbell, A. 1983. Growth of tagged American lobsters, *Homarus americanus*, in the Bay of Fundy. *Can. J. Fish. Aquat. Sci.* **40**: 1667–1675.
- Campbell, A. 1986. Migratory movements of ovigerous lobsters, *Homarus americanus*, tagged off Grand Manan, Eastern Canada. *Can. J. Fish. Aquat. Sci.* **43**: 2197–2205.
- Campbell, A., and A. B. Stasko. 1986. Movements of lobsters (*Homarus americanus*) tagged in the Bay of Fundy, Canada. *Mar. Biol.* **92**: 393–404.
- Cobb, J. S. 1969. Activity, growth and shelter selection of the American lobster. Ph.D. Thesis, University of Rhode Island, Kingston. 172 pp.
- Cooper, R. A. 1970. Retention of marks and their effects on growth, behavior, and migrations of the American lobster, *Homarus americanus*. *Trans. Am. Fish. Soc.* **99**: 409–417.
- Cooper, R. A., R. A. Clifford, and C. D. Newell. 1975. Seasonal abundance of the American lobster, *Homarus americanus*, in the Boothbay region of Maine. *Trans. Am. Fish. Soc.* **105**: 669–674.
- Cooper, R. A., and J. R. Uzmann. 1971. Migrations and growth of deep-sea lobsters, *Homarus americanus*. *Science* **171**: 288–290.
- Cooper, R. A., and J. R. Uzmann. 1980. Ecology of juvenile and adult

- Homarus*. Pp. 97-142 in *The Biology and Management of Lobsters*, Vol. 2, J. S. Cobb and B. F. Phillips, eds. Academic Press, New York.
- Ennis, G. P. 1972. Growth per moult of tagged lobsters (*Homarus americanus*) in Bonavista Bay, Newfoundland. *J. Fish. Res. Board Can.* **29**: 143-148.
- Ennis, G. P. 1984. Territorial behavior of the American lobster, *Homarus americanus*. *Trans. Am. Fish. Soc.* **113**: 330-335.
- Estrella, B. T. 1983. *Massachusetts Coastal Commercial Lobster Trap Sampling Program, May-November, 1981*. Tech. Rep. Massachusetts Div. Mar. Fish., Feb. 18, 1983. 80 pp.
- Estrella, B. T., and D. J. McKiernan. 1986. *Massachusetts Coastal Commercial Trap Sampling Program, May-November, 1985*. Tech. Rep. Massachusetts Div. Mar. Fish., July, 31, 1986. 73 pp.
- Hazlett, B., C. Bach, and C. Mitchell. 1977. Distribution patterns of the xanthid crab *Catalystodus floridanus* (Gibbes, 1850) (Decapoda Brachyura, Xanthidae). *Crustaceana* **33**: 316-319.
- Hudon, C. 1987. Ecology and growth of postlarval and juvenile lobster, *Homarus americanus*, off Iles de la Madeleine (Quebec). *Can. J. Fish. Aquat. Sci.* **44**: 1855-1869.
- Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* **52**: 225-247.
- Karnofsky, E. B., and J. Atema. 1979. Field and laboratory observations of lobster mating behavior. *Biol. Bull.* **157**: 374.
- Karnofsky, E. B., J. Atema, and R. Elgin. 1989. Field observations of shelter use, social behavior and foraging in the lobster, *Homarus americanus*. *Biol. Bull.* **176**: 000-000.
- Karnofsky, E. B., and H. J. Price. 1989. Dominance, territoriality, and mating in the lobster, *Homarus americanus*: a microcosm study. *Mar. Behav. Physiol.* (in press).
- Krouse, J. S. 1973. Maturity, sex ratio, and size composition of the natural population of American lobster, *Homarus americanus*, along the Maine coast. *Fish. Bull.* **71**: 165-173.
- Moriyasu, M. 1984. Lobster claw loss phenomena in Bideford River estuary, Prince Edward Island, Canada. *I.C.E.S. CM 1984/K:42* 1-21.
- Munro, J., and J.-C. Therriault. 1983. Migrations saisonnières du homard (*Homarus americanus*) entre la côte et les lagunes des Iles-de-la-Madeleine. *Can. J. Fish. Aquat. Sci.* **40**: 905-918.
- O'Neill, D. J., and J. S. Cobb. 1979. Some factors influencing the outcome of shelter competition in lobsters (*Homarus americanus*). *Mar. Behav. Physiol.* **6**: 33-45.
- Pezzack, D. S., and D. R. Duggan. 1986. Evidence of migration and homing of lobsters (*Homarus americanus*) on the Scotian shelf. *Can. J. Fish. Aquat. Sci.* **43**: 2206-2211.
- Phillips, B. F., J. S. Cobb, and R. W. George. 1980. General biology. Pp. 1-82 in *The Biology and Management of Lobsters*, Vol. 1, J. S. Cobb and B. F. Phillips, eds. Academic Press, New York.
- Scarratt, D. J. 1968. An artificial reef for lobsters (*Homarus americanus*). *J. Fish. Res. Board Can.* **25**: 2683-2690.
- Scarratt, D. J. 1973. Claw loss and other wounds in commercially caught lobsters (*Homarus americanus*). *J. Fish. Res. Board Can.* **30**: 1370-1373.
- Scrivener, J. C. E. 1971. Agonistic behavior of the American lobster, *Homarus americanus* (Milne-Edwards). *Fish. Res. Board Can. Tech. Rpt. No. 235*.
- Sheehy, D. J. 1976. Utilization of artificial shelters by the American lobster (*Homarus americanus*). *J. Fish. Res. Board Can.* **33**: 1615-1622.
- Sinclair, M. E. 1977. Agonistic behavior of the stone crab, *Menippe mercenaria* (Say). *Anim. Behav.* **25**: 193-207.
- Squires, H. J. 1970. Lobster (*Homarus americanus*) fishery and ecology in Port au Port Bay, Newfoundland, 1960-65. *Proc. Nat. Shellfish Assoc.* **60**: 22-39.
- Stewart, L. L. 1972. The seasonal movements, population dynamics and ecology of the lobster, *Homarus americanus* (Milne-Edwards), off Ram Island, Conn. Ph.D. Thesis. U. of Conn., Storrs. 112 pp.
- Tamm, G. R., and J. S. Cobb. 1978. Behavior and crustacean molt cycle: changes in aggression of *Homarus americanus*. *Science* **200**: 79-81.
- Templeman, W. 1935. Local differences in the body proportions of the lobster, *Homarus americanus*. *J. Biol. Board Can.* **1**: 213-226.
- Thomas, M. L. H. 1968. Overwintering of American lobsters, *Homarus americanus*, in burrows in Bideford River, Prince Edward Island. *J. Fish. Res. Board Can.* **25**: 2525-2527.
- Vannini, M. 1980. Notes on the behavior of *Ocypode ryderi* Kingsley (Crustacea, Brachyura). *Mar. Behav. Physiol.* **7**: 171-183.
- Wilder, D. G. 1953. The growth rate of the American lobster, *Homarus americanus*. *J. Fish. Res. Board Can.* **10**: 371-412.
- Wilder, D. G. 1963. Movements, growth, and survival of marked and tagged lobsters liberated in Egmont Bay, Prince Edward Island. *J. Fish. Res. Board Can.* **20**: 305-318.
- Wood, W. 1967. *Wood's New England's Prospect*. Burt Franklin, New York. 131 pp. (first published in 1865 by The Prince Society, Boston)
- Zawacki, C. S. 1971. An ecological study of the utility of auto tires as an artificial reef substrate in Shinnecock Bay. MS thesis, Long Island University Library.